How Systematic Age Underestimation Can Impede Understanding of Fish Population Dynamics: Lessons Learned from a Lake Superior Cisco Stock

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Abstract.—Systematic underestimation of fish age can impede understanding of recruitment variability and adaptive strategies (like longevity) and can bias estimates of survivorship. We suspected that previous estimates of annual survival (S; range = 0.20–0.44) for Lake Superior ciscoes *Coregonus artedi* developed from scale ages were biased low. To test this hypothesis, we estimated the total instantaneous mortality rate of adult ciscoes from the Thunder Bay, Ontario, stock by use of cohort-based catch curves developed from commercial gill-net catches and otolith-aged fish. Mean S based on otolith ages was greater for adult females (0.80) than for adult males (0.75), but these differences were not significant. Applying the results of a study of agreement between scale and otolith ages, we modeled a scale age for each otolith-aged fish to reconstruct catch curves. Using modeled scale ages, estimates of S (0.42 for females, 0.36 for males) were comparable with those reported in past studies. We conducted a November 2005 acoustic and midwater trawl survey to estimate the abundance of ciscoes when the fish were being harvested for roe. Estimated exploitation rates were 0.085 for females and 0.025 for males, and the instantaneous rates of fishing mortality were 0.089 for females and 0.025 for males. The instantaneous rates of natural mortality were 0.131 and 0.265 for females and males, respectively. Using otolith ages, we found that strong year-classes at large during November 2005 were caught in high numbers as age-1 fish in previous annual bottom trawl surveys, whereas weak or absent year-classes were not. For decades, large-scale fisheries on the Great Lakes were allowed to operate because ciscoes were assumed to be short lived and to have regular recruitment. We postulate that the collapse of these fisheries was linked in part to a misunderstanding of cisco biology driven by scale-ageing error.

Accurate age estimates are needed to promote sound fishery management (Beamish and McFarlane 1983). Systematic underestimation of fish age can lead to overestimates of growth and mortality rates and compromise understanding of year-class strength (Mills and Beamish 1980). Further, adaptations, such as low natural mortality (M), long life, and delayed age of maturity, can be masked when individual ages are underestimated (Mills and Beamish 1980; Beamish and McFarlane 1983). Biased growth and mortality estimates can in turn affect population modeling exercises used to formulate management advice on safe yield (Lai and Gunderson 1987; Tyler et al. 1989; Reeves 2003).

Van Oosten (1929) was the first to age ciscoes *Coregonus artedi* in the Laurentian Great Lakes using scales. Van Oosten (1929) did not validate this method for ciscoes, but had tested the method by aging aquarium-held lake whitefish *C. clupeaformis* known to be in their eighth or ninth year of life (Van Oosten 1923). Subsequent studies of ciscoes in the other Great Lakes used the Van Oosten (1929) method of scale aging; the estimated average ages in these studies always ranged between 2 and 6 years (Van Oosten 1930; Pritchard 1931; Scott 1951; Smith 1956; Dryer and Beil 1964). The populations were generally

composed of mixed year-classes, suggesting that variability in year-class strength was relatively low.

Reported annual survival rate (S) estimates developed from scale ages of ciscoes and the closely related bloater *C. hoyi* in the Great Lakes have also been low (ciscoes, 0.20–0.44: Selgeby 1982; Bowen et al. 1991; bloaters, ~0.23–0.32: TeWinkel et al. 2002). Studies comparing age estimates from scales and bony structures of individuals in the subfamily Coregoninae have reported that age estimates developed from otoliths and fin rays typically exceed scale-derived ages, especially for older otolith-aged fish (Aass 1972; Mills and Beamish 1980; Barnes and Power 1984). The problem with scale aging stems from fish living well beyond the age when somatic growth slows, so annuli formations on scale edges are difficult to identify (Aass 1972; Mills and Beamish 1980; Beamish and McFarlane 1983). In Lake Superior, an exceptionally large cisco year-class hatched in 1984 (MacCallum and Selgeby 1987) and provided managers an opportunity to evaluate scale aging techniques. As the 1984 cohort aged, it became clear that scale age estimates became increasingly inaccurate (D. Schreiner, Minnesota Department of Natural Resources, personal communication). By the late 1990s, all Lake Superior management agencies had switched to aging ciscoes with the otolith crack-and-burn method, but a formal evaluation of the validity of this aging method has not been attempted.

Several Lake Superior cisco stocks currently support roe fisheries. Determining the sustainability of these fisheries is a high research priority of management agencies (GLFC 2006). Determining sustainable harvest probably entails the development of stock-specific population models, and the success of these modeling endeavors will depend on accurate estimates of a number of parameters, including mortality rates. Estimates of total instantaneous mortality (Z) can be derived from catch curves (Ricker 1975) under the assumption that the fish are aged accurately (Mills and Beamish 1980), but quantifying the relative contribution of instantaneous fishing mortality (F) and M can be challenging (Pauly 1980). Estimates of F and M can be developed from tag recovery models (Brownie et al. 1985), but capturing and tagging a highly mobile species like ciscoes, which lose scales easily (Aass 1972), makes this approach tenuous. Alternatively, F can be estimated from the rate of exploitation (u), which can be calculated by dividing harvest by an estimate of population size (Ricker 1975). Acoustic methods have been used to estimate abundance of a number of pelagic species aggregated for spawning (Thorne et al. 1983; Hampton 1996; Thomas and Thorne 2003; Yule et al. 2006). In this study, we estimated (1) Z of a Lake Superior cisco stock with use of catch curves developed from commercial gill-net catch per effort (CPE) data and (2) F by comparing harvest with an estimate of at-large abundance developed from a fishery-independent acoustic survey. By subtraction, we estimated M as Z − F. Quantifying rates of different forms of mortality is an important first step in understanding the sustainability of roe fisheries.

The goals of this comparative study were to (1) reveal potential biases in scale-based estimates of Z and recruitment variability, (2) assess the validity of otolith age estimation for ciscoes in Lake Superior, and (3) explore how the application of scale aging shaped early understanding of cisco biology and the approaches used to manage commercial fisheries. To achieve these goals, we first estimated Z for otolith-aged adult male and female ciscoes based on CPE data collected from 1998 to 2005. We then used a comparative data set of otolith and scale ages to explore how our results changed depending on aging method. Next, we estimated F from the 2005 roe fishery using harvest and prespawner abundance data. Finally, we developed age distributions of at-large ciscoes from both otolith ages and modeled scale ages to examine which aging method provided the best agreement with an index of year-class strength calculated from a bottom trawl survey that has been conducted annually since 1988.

Methods

Since the early 1980s, fishers have targeted ciscoes in Thunder Bay, Ontario, for their roe mostly during November, when the fish form prespawning aggregations (Dextrase et al. 1986). Thunder Bay has been divided into three management zones (Figure 1), and the Ontario Ministry of Natural Resources (OMNR) sets total allowable commercial catches (TACCs) for each zone annually (Anonymous 2001). During 2005, the combined TACC for the three Thunder Bay zones equaled 170,000 kg.

Fishery-Dependent Data

Estimating annual harvest of year-classes.—Daily catch reports for each licensed operator were obtained from the Ontario Commercial Fisheries Association, Blenheim, and were used to estimate the annual biomass of ciscoes harvested from Thunder Bay. Through a partnership arrangement between the OMNR and the commercial industry, most commercial fishers provided the first 10 ciscoes caught in each net on each day. These "net-run" fish were placed in plastic bags with labels that identified the zones where nets were lifted, mesh size, landing date, and other information. Individual net-run fish were later given a unique identification number, sexed, and measured to
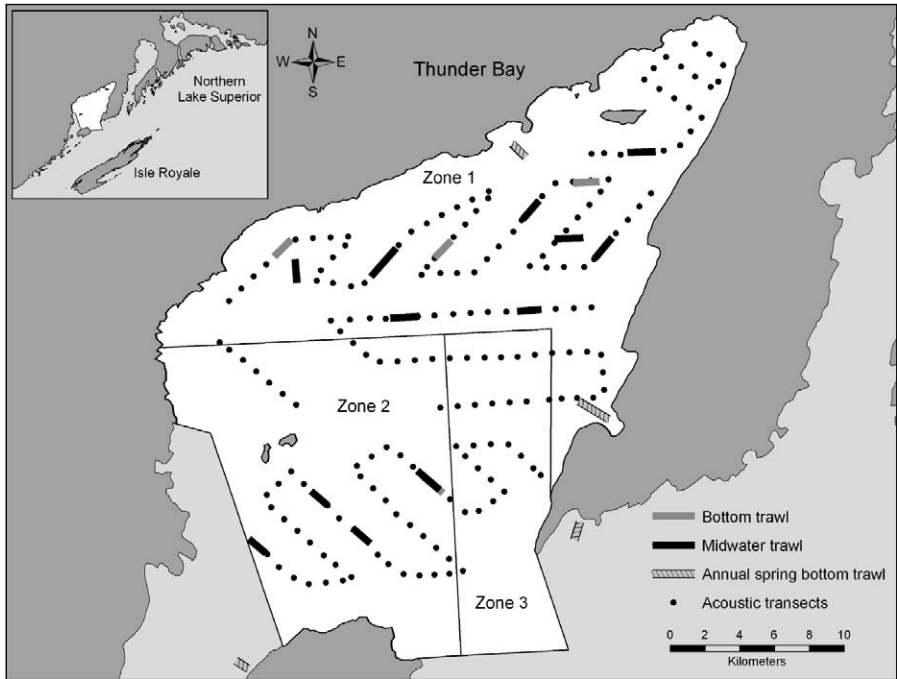
FIGURE 1.—Map of acoustic transects and trawl stations sampled at night to determine cisco spawner abundance and density during 13–17 November 2005 in Thunder Bay, Ontario. Boundaries of management zones 1–3 are shown, as are the locations of the annual spring bottom trawl stations used to develop the age-1 cisco recruitment index.

the nearest millimeter (fork length [FL] and total length [TL]), and most were weighed to the nearest gram. Otoliths were extracted and data for each fish were entered into a database. Because net-run fish were collected continuously throughout each fishing season, the fish in the database provide a representative sample of the commercial catch each year.

The net-run database spanning 1998 to 2005 included 10,749 individual fish records with 10,748 FLs, 8,281 TLs, and individual weight measurements. For fish in the database that had not been weighed directly, we predicted weights using length–weight relationships developed for each sex after pooling all 8 years of data (Table 1). We multiplied the proportions of male and female biomass in the database each year by the total estimated harvested biomass that year to estimate harvested biomass by sex. Total harvested

biomass of each sex was divided by the average weights of each sex to estimate numbers of males and females harvested in a given year.

Only subsamples of net-run fish were aged during each year; a total of 4,279 fish were aged (all by the same person) between 1998 and 2005. Up to 10 fish per 10-mm length-bin of each sex per zone per year were aged by the otolith crack-and-burn method (Schreiner and Schram 2001). When fewer than 10 fish belonged to a 10-mm length-bin, all were aged. When more than 10 were available, 10 were selected randomly from the total number in each length-bin. We pooled age data using 10-mm length-bins across the three management zones by year and developed sex-specific age–length keys, which we used to predict ages of all net-run fish in each year. We then apportioned annual male and female harvest estimates

TABLE 1.—Length–weight regressions for male and female ciscoes harvested from Thunder Bay, Ontario, between 1998 and 2005. The number of individuals used to develop each equation is indicated by N; R^2 is the coefficient of determination. Weight is in grams and total length (TL) is in millimeters.

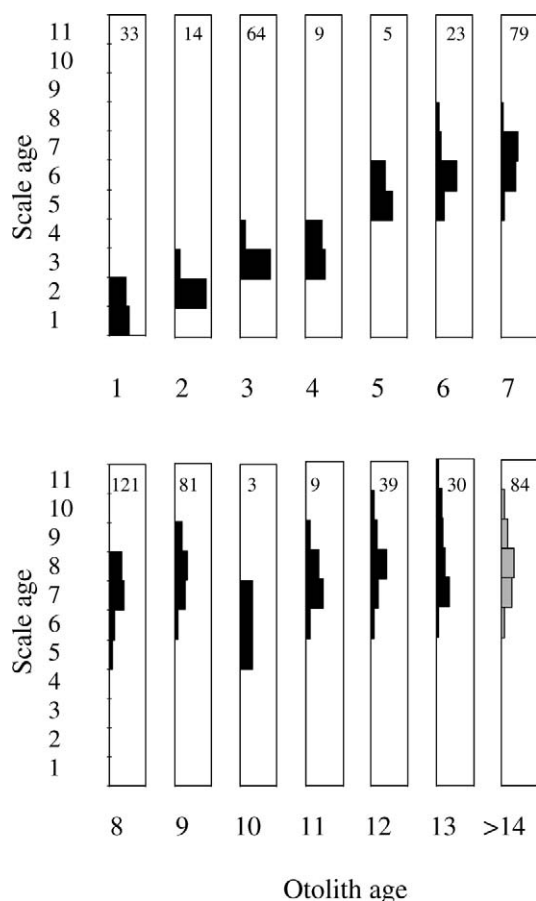| Sex	Equation	N	TL range (mm)	R^2
Male	$\log_e(\text{weight}) = -12.91 + (3.20 \times \log_e \text{TL})$	1,277	192–475	0.93
Female	$\log_e(\text{weight}) = -11.58 + (2.99 \times \log_e \text{TL})$	7,004	196–524	0.84

FIGURE 2.—Scale age distributions (black bars) for ciscoes of different otolith ages collected from Black and Thunder bays, Ontario, during 1997. For fish with otolith ages greater than 14, we pooled scale ages of all age-10 and older otolith-aged fish to estimate the distribution (gray bars). Numbers at the top of each plot represent fish sample sizes.

to year-classes, assuming that the net-run fish represented the entire annual catch.

Estimates of total instantaneous mortality based on otolith ages.—We estimated Z for both males and females from the slopes of least-squares linear regressions fitted to the descending right limbs of catch curves, each based on a single cohort (Ricker 1975; Van den Avyle and Hayward 1999). Our catch curve analysis was limited to the 1998–2005 commercial catch data because 1998 was the first year in which OMNR fully implemented the otolith crack-and-burn method. To ensure roe freshness, most nets were lifted after one night. For the rare net fished during multiple nights, we corrected effort by multiplying net length by nights fished before summing all effort. We plotted $\log_e$(CPE) (fish/m of net fished) of males and females

of each year-class in each year (1998–2005) to estimate Z ($Z = -$slope of linear regression). Estimates of Z were only reported for year-classes with descending limbs having a minimum of 4 years of data. The S was estimated as e^{-Z} (Ricker 1975).

The use of cohort-specific catch curves to estimate total mortality relies on three basic assumptions (Tuckey et al. 2007). First, it is assumed that catchability of the fishing gear remains constant from year to year. Second, catchability of a year-class is assumed to remain constant as the fish grows. Third, the catch curve is based on known CPE. We believe our data set meets all three of these assumptions. Fishers target females by suspending monofilament gill nets (constructed of a single mesh size) in the water column. A small range of mesh sizes was fished (79–89 mm, stretch measure) between 1998 and 2005, and the bulk of fish (91% by number) was taken with 83- and 86-mm mesh. Using otolith ages and lengths of ciscoes caught by midwater trawling during this study, we developed von Bertalanffy growth equations for males and females (U.S. Geological Survey [USGS], Great Lakes Science Center [GLSC], unpublished data). Based on these curves, we estimated that both males and females reach 90% of asymptotic length (L_∞) by age 5 and have negligible somatic growth after age 8. To avoid violating the first two assumptions, we only estimated Z for age-9 and older year-classes. Finally, because operators must report catches accurately or risk having their licenses revoked, we assumed that the commercial fishing records used to estimate CPE were accurate.

Estimates of total instantaneous mortality based on modeled scale ages.—We modeled how Z would have changed if the age–length keys had been developed from scales. We used results of a study examining agreement between otolith and scale ages (based on 513 individually aged ciscoes collected in Thunder and Black bays in 1997) to develop a modeled scale age for each otolith-aged fish in the 1998–2005 net-run database. We compiled a scale age distribution for each otolith age using the 1997 comparative data (Figure 2). Because few ciscoes aged with otoliths in 1997 exceeded 13 years (only 3 of 513 fish) and because the maximum otolith-aged fish from the net-run database was 21 years, we developed a scale age distribution for otolith ages of 14–21 years by pooling all scale ages of otolith-aged fish that were 10–13 years old in 1997 (Figure 2). To model a scale age for an otolith-aged individual, we randomly selected a scale age from the scale age distribution for that fish's otolith age. Using this method, the maximum modeled scale age was 11 years. We felt that this was a reasonable approach because all peer-reviewed studies of cisco

scale ages reported maximum ages ranging from 6 to 10 years (Van Oosten 1929; Smith 1956; Dryer and Beil 1964; Bowen et al. 1991). Modeled scale ages were used to construct age–length keys, and we repeated our previously described analysis to estimate Z.

Fishery-Independent Data

November 2005 acoustic and trawling surveys.— We estimated the rate of exploitation from fishing (u) of males and females by dividing numbers harvested during the November 2005 roe fishery by numbers at large obtained with a November 2005 acoustic and midwater trawl survey. We sampled Thunder Bay during the nights of 13–17 November 2005 using the USGS–GLSC RV *Kiyi*. Sampling occurred in a systematic fashion using a series of parallel acoustic transects spaced at roughly 3-km intervals (Figure 1). Acoustic data were collected using techniques identical to those described by Yule et al. (2006). Briefly, acoustic sampling occurred while traveling at speeds of 2.1–2.6 m/s. We used a BioSonics DT-X echosounder (BioSonics, Inc., Seattle, Washington) equipped with a 120-kHz, split-beam transducer with a half-power beam width of 6.7°. The transducer was deployed with a towbody to a depth of 1 m below the surface. The transducer emitted 3–5 pings/s, and pulse duration was set at 0.4 ms. Vessel position was measured with a differentially corrected Global Positioning System unit (accurate to 1 m), and survey path information was embedded in the acoustic data files.

Total fish densities (number/ha) were calculated for 10-m vertical cells over 1,000-m horizontal intervals using echo integration methods described by Yule et al. (2006). To estimate densities of large ciscoes (>250 mm TL), we multiplied total fish density in each cell by the proportion of single targets exceeding −35.6 decibels. Yule et al. (2006) showed that this approach maximized the correlation between acoustic density estimates of large fish in midwater trawl paths superimposed on echograms and actual catches of large ciscoes caught by trawling. We summed all the vertical cells down to the lake bed for each 1,000-m interval. To estimate total fish and large cisco abundances, we multiplied the arithmetic mean densities (using intervals as sample units) by the combined area of the three Thunder Bay management zones (66,579 ha). A geostatistical model developed by Petitgas and Lafont (1997) was used to estimate 95% confidence intervals (CIs) surrounding abundance estimates (see Yule et al. 2006 for details).

We assessed fish community composition at night by collecting 12 midwater trawl samples and 4 bottom trawl samples (Figure 1). The midwater trawl was fished at constant depths ranging from 3 to 42 m (headrope depth) below the surface. The midwater trawl had 15.2-m headrope and footrope lines and 13.7-m breast lines. The nylon mesh graduated from 152-mm stretch measure at the mouth to 13-mm stretch measure at the cod end. Bottom trawl samples were collected to confirm that most ciscoes occupied the pelagic zone at the time of our acoustic survey. The bottom trawl (3/4 Yankee trawl, number 35) had a 15.5-m headrope line, 11.9-m footrope line, and 2.2-m wing lines with 89-mm stretch measure at the mouth, 64-mm stretch measure at the trammel, and 13-mm stretch measure at the cod end. Only five ciscoes were caught in bottom trawl samples, indicating that at night, most ciscoes were occupying pelagic waters, where acoustic sampling is most effective.

Fish were sorted to species in the field, placed in plastic bags, iced, and processed the next day at the OMNR Thunder Bay Laboratory. Species were weighed in aggregate to the nearest gram. All individuals from small noncisco catches (<100 fish) and all ciscoes were measured to the nearest millimeter TL. For larger noncisco catches, 50–100 individuals were measured and the remaining fish were counted. The vast majority of ciscoes were weighed individually to the nearest 1 g and sexed, and reproductive state was assessed by examining their gonads (i.e., unknown; mature or immature males; and mature or immature females). Otoliths were extracted from trawl-caught ciscoes for aging, targeting 20 males and 20 females per 50-mm length-bin (range = 100–450 mm). The decision on how to sample trawl-caught ciscoes for development of age–length keys was made before the survey and was based on the project budget.

Because harvest is typically limited to November, we considered the Thunder Bay roe fishery to be a type 1 fishery (i.e., the population decreases during the fishing season because of catch removals only; Ricker 1975). The F for males and females was calculated using Ricker's equation for a type 1 fishery (i.e., $F = -\log_e[1 - u]$), where u is calculated by dividing the estimated number caught by the estimated number at large from the acoustic survey and midwater trawl samples. The value of M was calculated by subtraction (i.e., $M = Z - F$). For a type 1 fishery, the annual natural mortality rate (n) is calculated as $n = 1 - e^{-M}$ (Ricker 1975).

Assessment of cisco spawners is a new method, and there is much to learn about the temporal buildup of ciscoes on spawning sites (Yule et al. 2006). To explore whether most spawners had returned to Thunder Bay before our survey work, we plotted CPE (kg·net m^{-1}·night^{-1}) in commercial nets against landing date. We compiled plots for the 2005 fishing

TABLE 2.—Estimates of total fishing effort (gill-net m) and numbers and biomass (kg) of female and male ciscoes harvested in the Thunder Bay, Ontario, roe fishery, 1998–2005.

Year	Effort (gill-net m)	Females harvested		Males harvested	
		Number	Biomass (kg)	Number	Biomass (kg)
1998	137,700	340,000	169,000	54,000	22,000
1999	177,500	321,000	166,000	56,000	24,000
2000	170,600	336,000	181,000	34,000	16,000
2001	208,500	313,000	159,000	70,000	31,000
2002	278,200	359,000	179,000	74,000	32,000
2003	326,700	345,000	160,000	63,000	25,000
2004	248,600	306,000	132,000	54,000	21,000
2005	173,700	238,000	113,000	48,000	20,000

season for management zones 1 and 2 and omitted data from zone 3 because so few nets were set there. We limited the calculation of CPE to floating gill-net lifts fished for one night, and third-order polynomials were fitted to the plots to characterize trends.

Apportionment of cisco abundance estimates to different year-classes.—The acoustic abundance estimate of large ciscoes was apportioned to sizes and sexes based on midwater trawl catches. We first calculated for each trawl tow the relative proportions of males and females belonging to six groups (i.e., three size-groups each for males and females: 250–299, 300–349, and >350 mm TL) so that the proportions of all six groups in each trawl sample summed to 1.0. Using all the trawl tows as replicates, we calculated the average proportion for each group. We then multiplied these average six proportions by the acoustic abundance estimate of large ciscoes to estimate abundances of each group. These abundance estimates were then apportioned to year-classes based on age–length keys constructed using the same 50-mm length-bins for males and females.

To estimate abundances of small ciscoes (<250 mm TL), we multiplied the acoustic abundance estimate of fish smaller than 250 mm (i.e., total fish density − density of large ciscoes) by the proportional contribution of small ciscoes to the total midwater trawl catch of all fish smaller than 250 mm TL. We apportioned the estimated numbers of small ciscoes to age-classes based on a single age–length key developed from all trawl-caught ciscoes smaller than 250 mm TL that were aged.

Comparison of at-large ciscoes to an age-1 recruitment index.—The USGS–GLSC has sampled Thunder Bay annually since 1988 by bottom trawling, and densities of age-1 ciscoes (number/ha) serve as an index of year-class strength. Four fixed trawl stations (Figure 1) have been sampled during daylight hours in spring (May–June) using the same bottom trawl gear described previously.

To determine which aging method best tracked year-class strength, we compared the recruitment index data with age distributions of at-large fish during November 2005. If scale-based methods are correct, then no ciscoes survive past age 11. However, our otolith results showed that a large number of ciscoes at large during November 2005 were older. We compared the distribution of ciscoes older than age 11 (based on otolith ages) with the distribution of year-class strength to test the null hypothesis that aging based on scales was correct. If the null hypothesis is true, we would expect no relationship between the distributions of at-large year-classes based on otoliths and the recruitment index.

For the otolith-based at-large distribution, we summed the number of ciscoes of age 12 to 17 (i.e., 1988–1993 year-classes) and calculated the proportion that each year-class contributed to the total. Similarly, average density estimates of these same year-classes caught as age-1 fish were summed and the proportion each year-class contributed to that total was calculated. The metric used to measure the distance between the two distributions was the mean relative difference in proportions calculated as the mean of (proportion observed − proportion expected)/proportion expected (observed = at-large proportion; expected = recruitment index proportion). We added 0.01 to each of the expected values so that the divisor was not zero. We used a permutation test to assess the probability of obtaining the observed mean distance between the at-large and recruitment index proportions based on chance alone. There were 720 (i.e., calculated as 6!) possible permutations of the six at-large proportions.

Results

Commercial gill-net effort over the period 1998 to 2005 varied from 137,700 to 326,700 m of suspended gill net (Table 2). The numbers of females harvested each year exceeded 300,000 except during 2005. A fisher violated a regulation during 2005 and his license

was suspended during the fishing season, so the harvested biomass (133,000 kg) was below the combined TACC of 170,000 kg. During all years, fewer males (34,000–74,000; Table 2) were harvested than females (238,000–359,000).

Estimates of Total Instantaneous Mortality Based on Otolith Ages

We only estimated Z for cohorts hatched between 1984 (age 21 in 2005) and 1996 (age 9 in 2005) because catch curves for younger year-classes still had ascending right limbs, providing evidence that these year-classes had not fully recruited to commercial gill nets. For males, nine year-classes met our criteria of having descending limbs with a minimum of 4 years of data (Figure 3); for females, 10 year-classes met the criteria (Figure 4). Among the nine year-classes for which Z could be estimated for both males and females (Table 3), the average estimate was 0.29 (SD = 0.08) for males and 0.22 (SD = 0.11) for females; these Z-estimates translate to estimated mean annual S of 0.75 for males and 0.80 for females. A paired t-test showed that Z-estimates for males and females of the nine year-classes did not vary significantly ($t = -1.30$; df = 8; $P = 0.23$).

Estimates of Total Instantaneous Mortality Based on Modeled Scale Ages

We were able to estimate Z for males and females belonging to six modeled year-classes (1990–1995; Table 3). Declining limbs of catch curves for both males (Figure 3) and females (Figure 4) constructed with modeled scale ages were steeper than those developed with otolith ages. Average estimates of Z for males and females developed from modeled scale ages (Table 3) were 1.03 and 0.89, respectively. A paired t-test showed that Z-estimates for males and females based on modeled scale ages did not vary significantly ($t = -1.45$; df = 5; $P = 0.21$). From modeled scale ages, we estimated mean annual S of 0.36 for males and 0.42 for females.

We compared Z-estimates for males and females based on the four year-classes with otolith and scale age estimates (1990, 1991, 1993, and 1994; Table 3) and found significant differences for both males ($t = 12.14$; df = 3; $P < 0.01$) and females ($t = 18.11$; df = 3; $P < 0.001$).

November 2005 Fishery-Independent Survey and Exploitation Rates

The pattern of cisco CPE in commercial nets versus landing date showed that our acoustic and trawling work occurred at a time when commercial catch rates were relatively high (Figure 5), suggesting that most spawning-size ciscoes had returned to Thunder Bay before our survey. Thus, we are confident that our estimates of adult numbers reflect the prespawning population subjected to exploitation.

Midwater trawling captured 730 ciscoes. Ciscoes represented 17% of captured fish less than 250 mm TL and 96% of fish exceeding this length. Of the males smaller than 250 mm TL, 39% were sexually mature, whereas only 12% of the small females were mature. Examination of gonads showed that 93% of males and 95% of females larger than 250 mm TL were sexually mature.

The arithmetic mean total fish density from our acoustic sampling was 890 fish/ha, and the density of large (>250-mm) ciscoes was 78 fish/ha. We estimated total pelagic fish abundance in Thunder Bay at 59.1 million (95% CI = 52.9–65.4 million) and the abundance of large ciscoes at 5.2 million (95% CI = 4.3–6.2 million). The estimated density of ciscoes smaller than 250 mm TL was 140 fish/ha.

A total of 196 ciscoes captured by midwater trawling from Thunder Bay were aged by the otolith crack-and-burn method (Table 4). Of this total, 85 were males, 106 were females, and the sex of five age-0 fish (<129 mm TL) could not be determined. Trawl-captured males were predominantly age 2 (2003 year-class; 35%) and age 7 (1998 year-class; 46%); the oldest males were age 17 (1988 year-class). Females caught by midwater trawling were predominantly age 2 (24%), age 7 (41%), and age 17 (11%). The oldest female was age 21 (1984 year-class).

After applying age–length keys, three distinct age groupings were evident in the at-large age distribution, and there were gaps between them (Figure 6A). We used the gaps to define three year-class groupings (1984–1992, 1993–1999, and 2000–2005). We summed the total number of at-large fish in each grouping that were harvested (Figure 6B), and we used these estimates to calculate u for each grouping (Figure 6C). The u of both males and females belonging to the youngest grouping was less than 0.1%. We estimated u of the 1993–1999 year-class group at 2.3% for males and 8.0% for females. For the oldest year-class group (1984–1992), u was 4.6% for males and 10.0% for females. We combined data for the two oldest groups (i.e., market size) and calculated percent mortality at 2.5% for males and 8.5% for females. With the latter estimates of u, F was estimated at 0.025 and 0.089 for market-size males and females, respectively. The M for market-size fish equaled 0.265 for males and 0.131 for females; n of males and females was 23% and 12%, respectively.

When we used modeled scale ages to apportion the
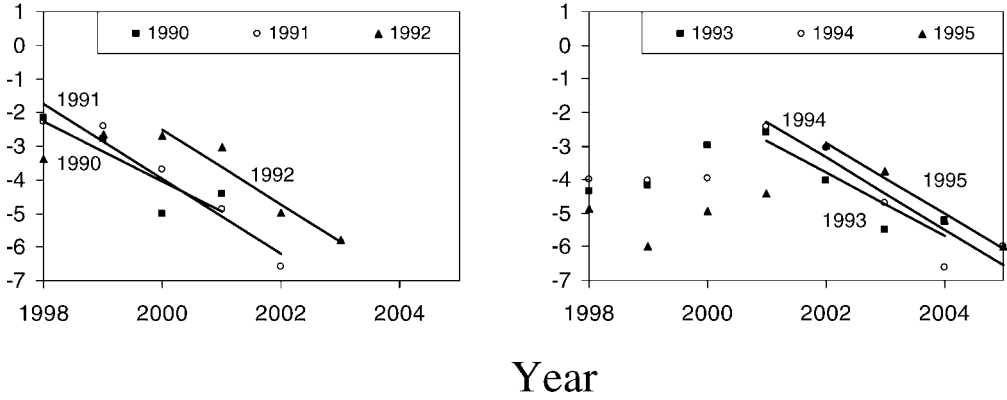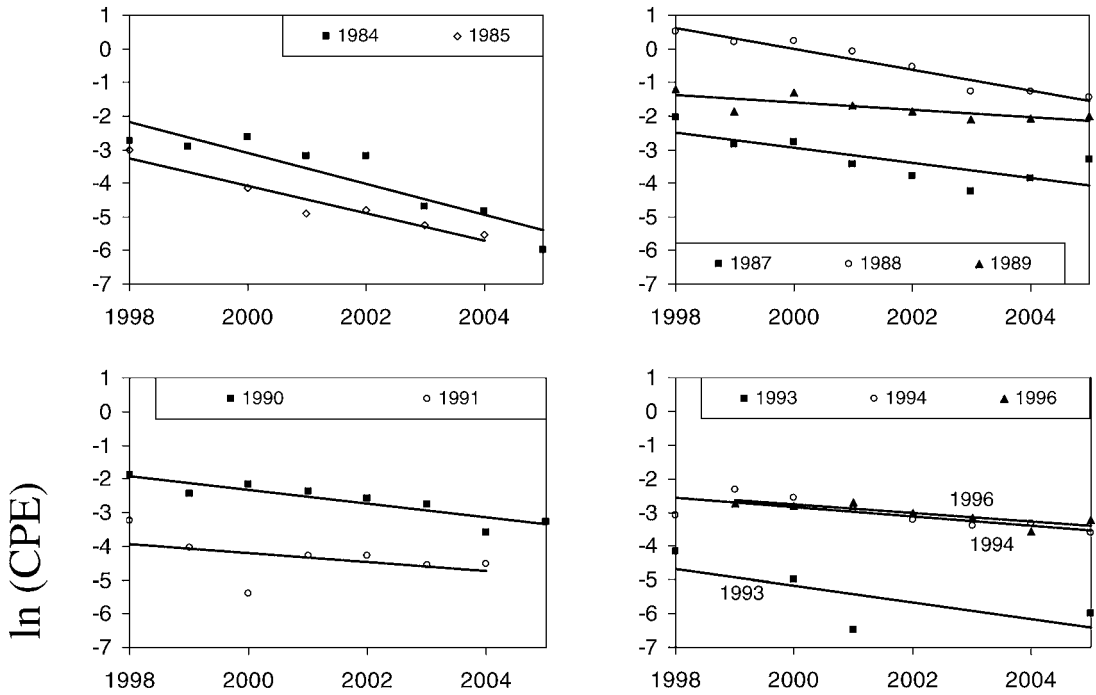
Otolith ages
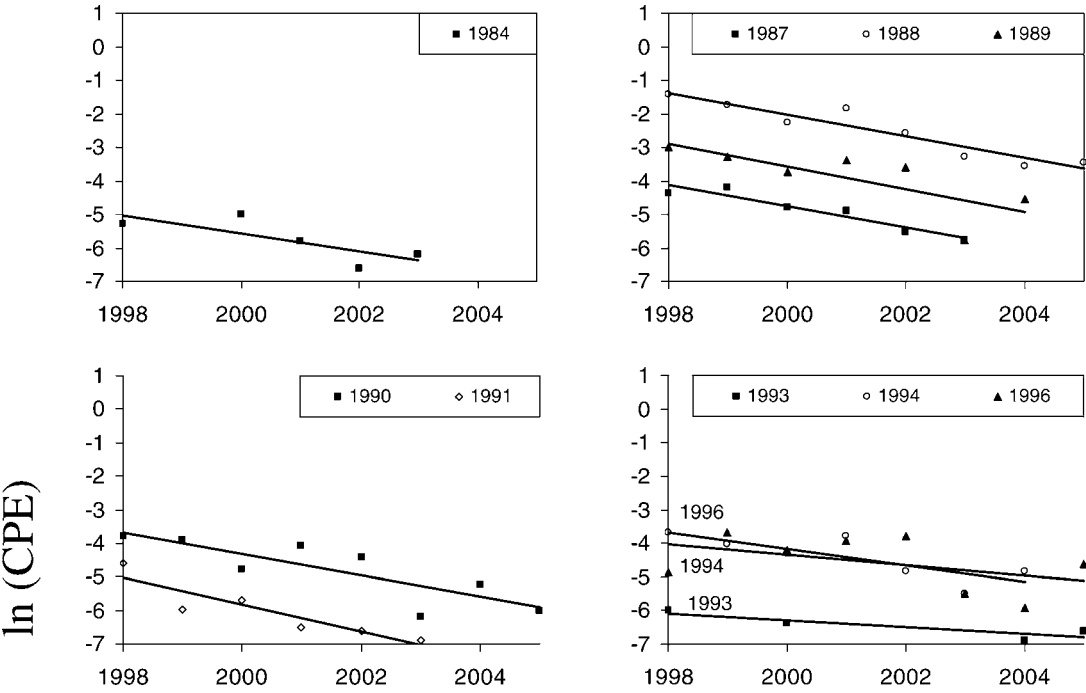
Modeled scale ages

FIGURE 3.—Catch curves ($\log_e$[catch per effort, CPE, in fish/m]) developed from otolith ages of male ciscoes from nine year-classes caught by commercial gillnetting in Thunder Bay, Ontario, 1998–2005. Lines represent least-squares linear regression models fitted to data from each year-class (some lines are labeled to distinguish year-classes with overlapping or similar data); the slope of each line represents the instantaneous total mortality rate (Z; Table 3). Catch curves developed from modeled scale ages of males from six year-classes are also presented (bottom panels).

November 2005 acoustic and harvest estimates to year-classes, the strong 1988 and 1989 year-classes detected by otolith aging techniques were no longer at large or represented in the fishery (Figure 7). Based on modeled scale ages, one might conclude that relatively strong cisco year-classes recruited each year between 1996 and 1999 (Figure 7A), which leads to a very different interpretation than otolith ages that show the 1998 year-class to be the only cohort of any significance to recruit during the latter half of the 1990s (Figure 6A).

Otolith ages

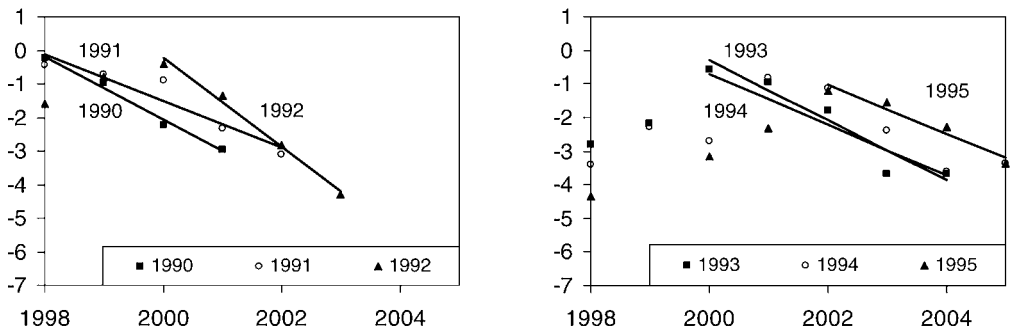## Modeled scale ages

Year

FIGURE 4.—Catch curves ($\log_e$[catch per effort, CPE, in fish/m]) developed from otolith ages of female ciscoes from 10 year-classes caught by commercial gillnetting in Thunder Bay, Ontario, 1998–2005. Lines represent least-squares linear regression models fitted to data from each year-class (some lines are labeled to distinguish year-classes with overlapping or similar data); the slope of each line represents the instantaneous total mortality rate (Z; Table 3). Catch curves developed from modeled scale ages of females from six year-classes are also presented (bottom panels).

Comparison of At-Large Ciscoes to an Age-1 Recruitment Index

The estimated density of age-1 ciscoes exceeded 10 fish/ha in only 4 of the 17 years of the recruitment time series (1989, 1990, 1998, and 2003 year-classes; Figure 8). When otolith ages were used to develop age–length keys, we found that these same strong year-classes were at large during the November 2005 fishery-independent survey, whereas weak or absent year-classes were not.

The relative observed proportions of 12–17-year-old ciscoes at large during 2005 based on otolith ages were

TABLE 3.—Estimates of instantaneous total mortality rate (Z) and annual survivorship rate (S) of male and female ciscoes from different year-classes (1984–1996) in Thunder Bay, Ontario. Estimates were derived using age–length keys developed from otolith-aged fish and modeled scale ages. The number of years in descending limbs of catch curves used to calculate Z is in parentheses.

| | Otolith ages | | | | Modeled scale ages | | | |
| | Male | | Female | | Male | | Female | |
Year-class	Z	S	Z	S	Z	S	Z	S
1984	0.26 (5)	0.77	0.46 (8)	0.63	—	—	—	—
1985	—	—	0.41 (6)	0.66	—	—	—	—
1986	—	—	—	—	—	—	—	—
1987	0.32 (6)	0.73	0.22 (8)	0.80	—	—	—	—
1988	0.32 (8)	0.73	0.31 (8)	0.73	—	—	—	—
1989	0.34 (7)	0.72	0.11 (8)	0.90	—	—	—	—
1990	0.32 (8)	0.73	0.21 (8)	0.81	0.90 (4)	0.41	0.94 (4)	0.39
1991	0.40 (6)	0.67	0.14 (7)	0.87	1.11 (5)	0.33	0.70 (5)	0.50
1992	—	—	—	—	1.12 (4)	0.33	1.32 (4)	0.27
1993	0.10 (4)	0.90	0.25 (4)	0.78	0.94 (4)	0.39	0.89 (5)	0.41
1994	0.24 (7)	0.78	0.14 (8)	0.87	1.07 (5)	0.34	0.76 (5)	0.47
1995	—	—	—	—	1.05 (4)	0.35	0.72 (5)	0.49
1996	0.28 (7)	0.76	0.13 (7)	0.88	—	—	—	—
Average[a]	0.29	0.75	0.22	0.80	1.03	0.36	0.89	0.42
SD[a]	0.08	0.06	0.11	0.09	0.09	0.03	0.23	0.09

[a] Based only on year-classes with estimates for both males and females.

0.05 for the 1993 year-class, 0.00 for the 1992 year-class, 0.04 for the 1991 year-class, 0.13 for the 1990 year-class, 0.21 for the 1989 year-class, and 0.57 for the 1988 year-class. The relative proportions of age-1 recruits were 0 for the 1993 year-class, 0.02 for the 1992 year-class, 0.03 for the 1991 year-class, 0.46 for the 1990 year-class, 0.40 for the 1989 year-class, and 0.09 for the 1988 year-class. For these observed distributions, the mean relative difference was 1.81 (Figure 9). For all possible 720 permutations of numbers at large, the mean relative difference between proportions ranged from 0.4 to 11.3 and the overall mean was 4.6 (Figure 9). The permuted differences

were less than the observed mean relative distance 17% of the time; in other words, there was a 17% chance that numbers at large and the recruitment index were distributed with greater similarity based on chance alone. Alternatively, we are 83% confident in rejecting our null hypothesis that age-specific numbers of at-large ciscoes based on scale ages were correct.

Discussion

The underestimation of age in long-lived fish based on examination of scales is a well-documented problem (Aass 1972; Beamish and McFarlane 1983; Barnes and Power 1984). Studies generally report good agreement between scale ages and bony structure (otoliths or fin rays) ages in young fish when somatic growth is rapid. However, agreement becomes progressively worse as fish age because fewer annuli are discernable on scales (Mills and Beamish 1980; Barnes and Power 1984; Frie et al. 1989; Rocha-Olivares 1998). Mills and Beamish (1980) studied lake whitefish and concluded that scale aging was acceptable for heavily exploited populations, as did Frie et al. (1989) for a fast-growing and heavily exploited population of walleyes *Sander vitreus*. Using otolith age estimates, we found that ciscoes belonging to the Thunder Bay stock exhibited rapid growth in their first 5–8 years of life. Growth after age 8 was negligible, but individuals can survive for an additional 10 or more years with little somatic growth. Given the difficulty in using scales to estimate age in older fish, we believe that the decision made by Lake Superior fisheries managers to begin aging
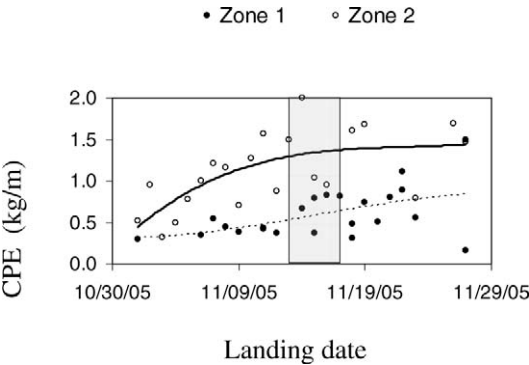

FIGURE 5.—Cisco catch per effort (CPE; kg/gill-net m) in floating commercial nets within management zones 1 and 2 of Thunder Bay, Ontario (see Figure 1), during the November 2005 roe fishery. The shaded rectangle indicates the time frame of our acoustic and trawling survey.

TABLE 4.—Age–length keys developed for otolith-aged male and female ciscoes caught by midwater trawling from Thunder Bay, Ontario, 13–17 November 2005. Column headings are year-class (most recent [2005] to least recent [1984]) and corresponding age (0–21 years; in parentheses).

Length bin (mm)	05 (0)	04 (1)	03 (2)	02 (3)	01 (4)	00 (5)	99 (6)	98 (7)	97 (8)	96 (9)	95 (10)	94 (11)	93 (12)	92 (13)	91 (14)	90 (15)	89 (16)	88 (17)	87 (18)	86 (19)	85 (20)	84 (21)
Males																						
<250	4	1	20	1																		
250–299			10																			
300–349							2	31	1	1								1				
≥350								8		1							1	3				
Male subtotal	4	1	30	1	0	0	2	39	1	2	0	0	0	0	0	0	1	4	0	0	0	0
Females																						
<250			20	4				1														
250–299			5	2			1	4														
300–349				1			1	21	1	1			1			2		1				
≥350								17	1	2		1			1	1	5	11				1
Female subtotal			25	7			2	43	2	3	0	1	1	0	1	3	5	12	0	0	0	1
Total	4	1	55	8			4	82	3	5	0	1	1	0	1	3	6	16	0	0	0	1

ciscoes with otoliths is already leading to a better understanding of cisco biology.

Beamish and McFarlane (1983) stressed the importance of validating techniques used to age fish because inaccurate ages can cause serious problems in the management of fish populations. A number of different approaches have been used to validate aging practices, including tagging studies (Aass 1972; Newman et al. 1996), injection of fluorescent marks on growing calcified structures (de Pontual et al. 2006), and bomb radiocarbon methods (Piner et al. 2005). A major weakness of our study is we had no known-age fish to validate our otolith aging method explicitly. When age
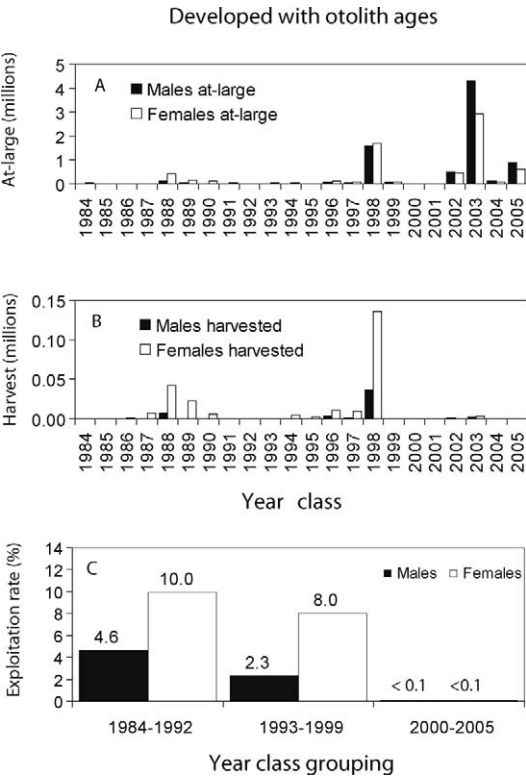

FIGURE 6.—Estimated numbers of male and female ciscoes of different year-classes (based on otolith ages) that were (A) at large and (B) harvested from Thunder Bay, Ontario, during the November 2005 roe fishery. Note that the y-axis scale is different for each graph. (C) Exploitation rates (%) for males and females of three year-class groupings are presented.
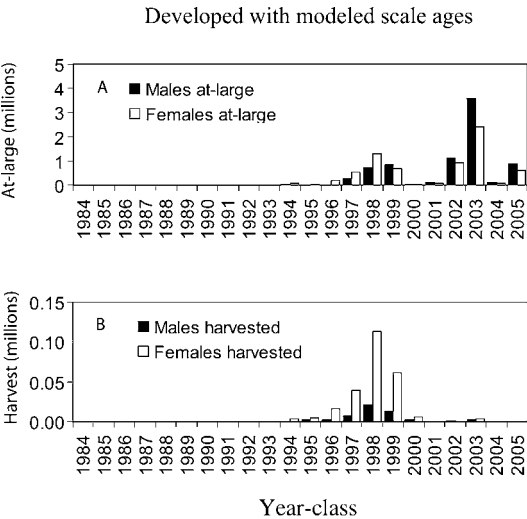

FIGURE 7.—Estimated numbers of male and female ciscoes of different year-classes (based on modeled scale ages) that were (A) at large and (B) harvested from Thunder Bay, Ontario, during the November 2005 roe fishery.
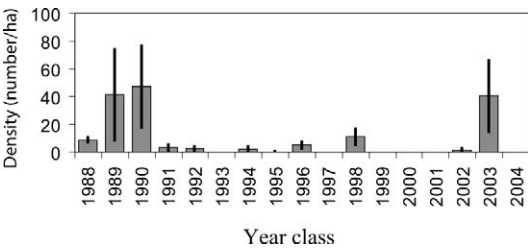
FIGURE 8.—Mean density (±SE; number/ha) versus year of hatch for age-1 ciscoes sampled by daytime bottom trawling during spring (May–June) at four fixed stations in Thunder Bay, Ontario, 1989–2005.
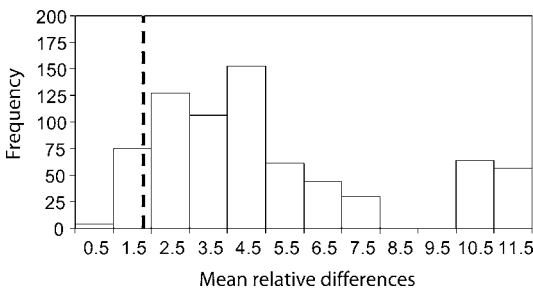

FIGURE 9.—Distribution of mean relative differences from a permutation test (based on 720 permutations; see Methods) used to assess the probability that the mean difference between the observed proportions of at-large ciscoes from the 1988–1993 year-classes (based on otolith ages) in Thunder Bay, Ontario, and the recruitment index (proportion of average age-1 density contributed by each year-class) was based on chance alone. The overall mean difference (1.81) is indicated by the solid dashed line.

distributions of 12–17-year-old otolith-aged ciscoes were compared with past measures of their year-class strength, we found good agreement. This finding is strong evidence, albeit not unequivocal, that otolith age estimates were accurate. Validating our aging method by conducting a tagging study would be challenging given the propensity of ciscoes to lose scales (Aass 1972). However, recent live releases of fragile European hake *Merluccius merluccius* using specially designed trawl cod ends show that this obstacle is not insurmountable (de Pontual et al. 2006). The fact that the preferred bony structure for estimating age of ciscoes (otoliths) cannot be removed nonlethally is probably the biggest challenge to overcome. The approach of de Pontual et al. (2006) to apply an external tag to promote later recovery, coupled with a nonlethal means of putting a mark on calcified structures (e.g., injecting fish with a solution of oxytetracycline) to verify annuli production, seems the most logical strategy to further validate cisco aging methods.

When we used otolith ages to develop catch curves, the derived estimates of S for spawning-size male (0.75) and female (0.80) ciscoes were far greater than previous estimates developed for the species in Lake Superior. For ciscoes collected near Cornucopia, Wisconsin, Selgeby (1982) estimated S from scale ages at 0.20 and 0.31 (both sexes) during the 1950s, when commercial harvest was deemed excessive. Using scale ages, Bowen et al. (1991) estimated mean S at 0.44 for male ciscoes and 0.35 for female ciscoes at three sites in U.S. waters of Lake Superior after commercial fishing had largely ceased. When we used modeled scale ages to estimate S, we obtained values (males = 0.36; females = 0.42) that were within the range reported in these previous studies. Our modeling suggests the low historic S may have been driven more by systematic age underestimation and less by factors operating on the fish populations when the data were gathered. Consistent with our modeling effort, Mills

and Beamish (1980) estimated a mean S of 0.46 using lake whitefish scale ages and 0.68 using fin ray age estimates. We conclude that ciscoes in Lake Superior live to much older ages and have much lower mortality rates than previously thought.

In this study, we found that adult female ciscoes were more abundant than adult males in the Thunder Bay stock, even after years of being selectively harvested (Tables 2, 4). Our preliminary estimates of n for males (23%) and females (12%), based on 1 year of data, suggest that this pattern is driven by the lower rate of natural mortality of females compared with males. Differential S between the sexes is common among fish species; higher survival of females has been reported for jackass morwongs *Nemadactylus macropterus* (Wankowski et al. 1988), white grunts *Haemulon plumierii* (Murie and Parkyn 2002), Pacific red snapper *Lutjanus peru* (Rocha-Olivares 1998), and bloaters (TeWinkel et al. 2002). The study by Bowen et al. (1991) was conducted because of management concerns that departures from 50:50 sex ratios found in some Lake Superior cisco fisheries during the late 1970s were impeding population recovery. Using scale ages, these authors found that total mortality rates of females and males did not vary significantly; using a population model, they concluded that female predominance was probably linked to the production of fewer male progeny (possibly through sexual differentiation of juveniles) under low-density situations. TeWinkel et al. (2002) attributed female predominance in Lake Michigan bloaters during the 1990s to differential mortality across sexes and several years of poor recruitment. We propose that female predominance among Lake Superior ciscoes is not an abnormal state

but arises from males having a lower S than females. Similar to findings by TeWinkel (2002) for bloaters, our results indicate that cisco populations will tend to be composed of more adult females after years of poor recruitment.

Recruitment data on Lake Superior cisco stocks have been reported in a number of studies (Dryer and Beil 1964; MacCallum and Selgeby 1987; Bronte et al. 2003; Hoff 2004). Dryer and Beil (1964) used scales to age ciscoes caught in gill nets over a 10-year period, when yields were still high (1950–1959); they reported that age-4 fish dominated the catches each year in four different areas of Lake Superior. They also reported that the strongest and weakest year-classes recruiting between 1946 and 1955 only varied twofold, evidence for near-constant recruitment. Based on modeled scale ages, we have shown how one strong year-class can suddenly become multiple year-classes with the introduction of scale aging error. Our modeling work casts doubt on the findings of Dryer and Beil (1964) that Lake Superior ciscoes had, at one time, fairly stable recruitment. MacCallum and Selgeby (1987) were the first authors to report information on cisco year-class strength in Lake Superior based on the capture of juveniles. During assessment fishing from 1958 to 1972, a trivial number of juvenile ciscoes were captured. However, after 1974, catches increased sharply but with high interannual variability in year-class strength (MacCallum and Selgeby 1987). More recent cisco recruitment data spanning 1978 to the present continue to show a pattern of highly variable recruitment and the occurrence of strong year-classes at sporadic intervals (Bronte et al. 2003; Hoff 2004; this study). This recruitment pattern has been described as "poor" (Bronte et al. 2003) and "very poor" (Hoff 2004). Our work suggests that the use of these modifiers is unwarranted because stable recruitment, as reported by Dryer and Beil (1964), probably never occurred.

Using scale aging methods, most early investigations concluded that ciscoes in the Great Lakes were short lived and had fairly constant recruitment levels (Van Oosten 1929, 1930; Pritchard 1931; Smith 1956; Dryer and Beil 1964). The age distributions developed from modeled scale ages of harvested males and females approached a normal distribution (Figure 7B), quite similar in shape to age distributions reported in most historic studies. From our review of the historic literature, it seems that commercial fisheries were viewed as a reasonable means of capitalizing on vast populations that would suffer high mortality even without fishing. Cisco populations collapsed in all of the Great Lakes during the 20th century, and overfishing was often cited as the most likely cause (Smith 1968; Berst and Spangler 1972; Christie 1972;

Hartman 1972; Lawrie and Rahrer 1972; Wells and McLain 1972). It is interesting to consider the role that systematic age underestimation may have played in the demise of these stocks. On one hand, it is plausible that past aging data were reasonably correct and that only young fish were present in these populations because older, larger individuals were removed by size-selective gill nets. On the other hand, older ciscoes were present and the importance of their longevity was masked by aging error. It is our opinion that past inferences about longevity and recruitment variability were erroneous owing to (1) scale aging error and (2) the tendency of past researchers to only examine adult fish caught in gill nets while devoting little or no attention to capturing new recruits. Van Oosten (1929) assumed that because known-age lake whitefish in a New York aquarium could be aged accurately with scales, so too could wild ciscoes. This assumption was adopted in subsequent studies and, not surprisingly, similar conclusions were reached about cisco population dynamics. If the aquarium-held lake whitefish examined by Van Oosten (1929) had been age 20, might the history of the Great Lakes cisco fisheries, some of the largest ever to exist in freshwater, have unfolded differently?

Acknowledgments

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